

HEPATICA IN NORTH AMERICA

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For many years North American botanists have accepted the maintenance of two species of *Hepatica* in the United States and Canada, *H. acutiloba* DC. and *H. americana* (DC.) Ker. This division into distinct specific taxa has been continued in the current eighth edition of Gray's Manual. However, Gleason, in the New Illustrated Flora (vol. 2: 183. 1952) has questioned the soundness of the recognition of *H. americana* as a species distinct from *H. nobilis* Schreb. of Europe, noting that "The difference between our plant and the European *H. nobilis* Schreb. is slight and scarcely warrants specific segregation." It is the purpose of the present paper to provide further support of Gleason's suggestion, and to bring evidence to indicate that the American taxa of *Hepatica* are better considered as varieties of the European *H. nobilis*.

PRELIMINARY OBSERVATIONS

North American *Hepaticas* fall naturally into two taxa, 1) those with rounded lobes of the leaf-blades, and 2) those with acute or acutish lobes. These obvious differences have been the chief criteria used to distinguish the taxa specifically. Over most of the North American range of the genus, the two taxa occupy usually separate and distinct habitats, the populations of the two taxa maintaining themselves rather uniformly, not only ecologically but also geographically. In Missouri, for example, *H. acutiloba* DC. occupies the more neutral to calcareous soils, *H. americana* the more acid soils, and *H. acutiloba* occupies glaciated northern Missouri extending west in that sector to Mercer and Sullivan counties, whereas *H. americana* is restricted to unglaciated Ozarkian southern Missouri. The ranges of the two taxa in Missouri are fairly sharp, but at their zones of overlap geographically and ecologically intergrading specimens of hybrid origin are encountered (Fig. 1). In northern Illinois, where the margins of the ranges also overlap, intermediate types are found which are impossible to assign to one or the other of the two taxa.

The problem of the recognition of the two taxa as distinct

species presented itself to the present authors in 1943. Both "species" occurred by the thousands on the forested morainal slopes and crests of the ravines of the Valparaiso Moraine in the area where the authors lived in the Biltmore subdivision of Barrington, Lake County, northern Illinois. The opportunity of intensive study of this problem was offered the junior author, who intensively surveyed the living flowering plants throughout a three-mile length of the stream

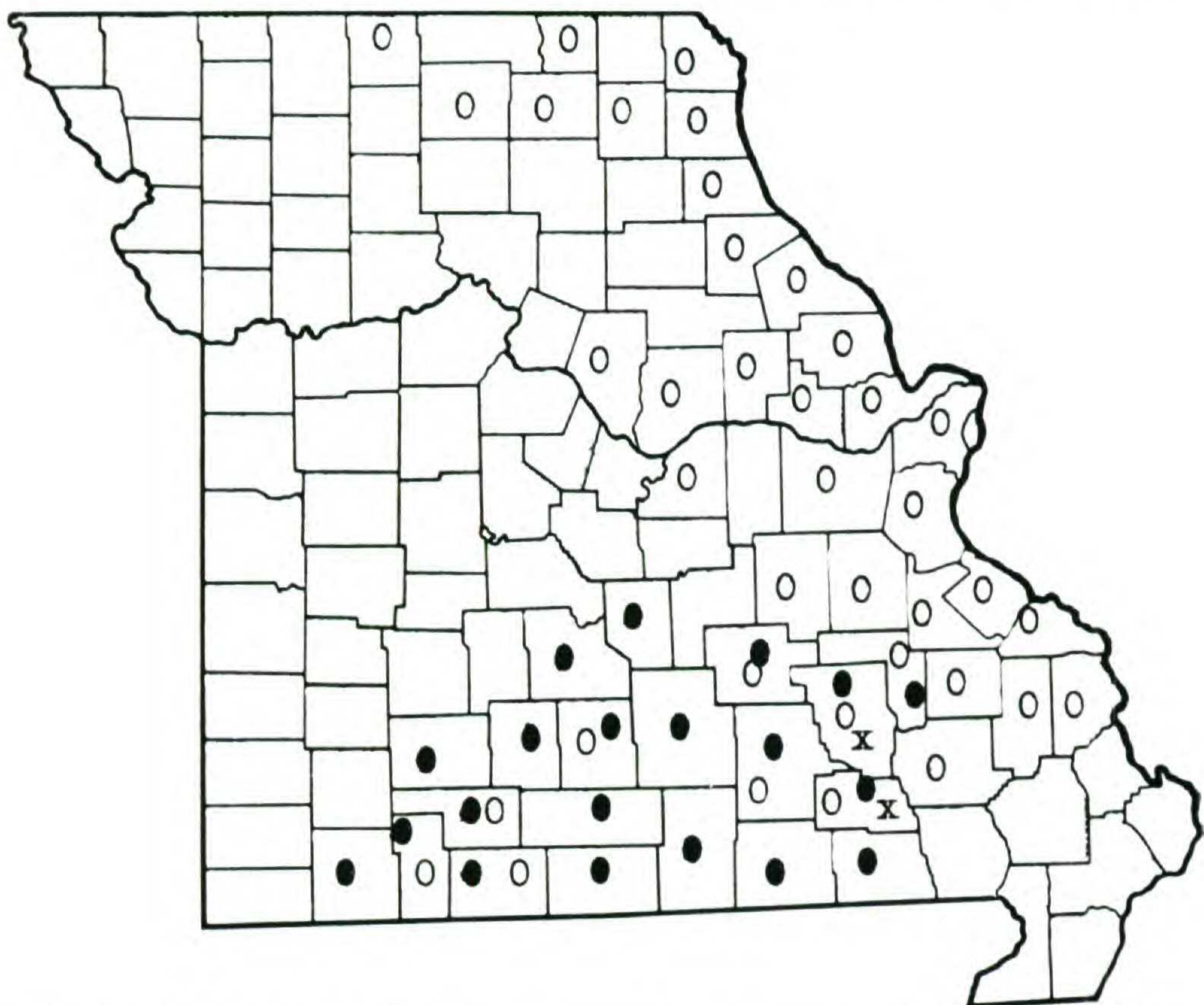


FIG. 1. Distribution of *Hepatica* in Missouri. Solid oval — *H. nobilis* var. *obtusa*. Open oval — *H. nobilis* var. *acuta*. X — putative hybrid populations.

following Eton Drive in the wooded section of Biltmore subdivision. In this area *H. americana* occurred on the more acid, leached soils on top of the ravines and slopes, whereas *H. acutiloba* was encountered most frequently in the richer and more neutral soil of the creek bottom and ascended to nearly three-fourths the distance up the slope. A zone of overlap existed in the upper portion of the slope where the two types met. Study of all the plants in this extensive area, based upon apex of leaf-blades and involucre, revealed an intergradation of the two taxa, showing the following results: 35% pure *H. americana*, 15% pure *H. acutiloba*, with

the remaining 50% somewhere between the two and often too puzzling to determine as one or the other "species." No additional facts could be obtained from study of the color, number, length, or width of the sepals. Their color varied from pale lavender to deep purple in 90% of the plants examined, pale pink to deep rose in about 5% of the cases, and white in another 5%. Both taxa exhibited approximately the same percentage differences. Moreover, no distinction could be found among either *H. acutiloba* or *H. americana* in color variation nor in their occurrence on any particular exposure of slope.

Measurements of involucre and sepals of living plants from the above area revealed the following: *Sepal length*: 9-13 mm. long in *H. americana*, averaging 11.6 mm.; 10-15 mm. long in *H. acutiloba*, averaging 11.75 mm.; 11-14 mm. long in the intermediate types, averaging 12.05 mm. *Sepal width*: 5.5-8 mm. wide in *H. americana*, averaging 6.5 mm.; 4-8 mm. wide in *H. acutiloba*, averaging 6.75 mm.; 5.5-10 mm. wide in the intermediate types, averaging 7.15 mm. *Involucre length*: 9-17 mm. long in *H. americana*, averaging 12.3 mm.; 7-18 mm. long in *H. acutiloba*, averaging 11.4 mm.; 9-14 mm. long in the intermediate types, averaging 11.4 mm. *Involucre width*: 7.5-9 mm. wide in *H. americana*, averaging 7.25 mm.; 4-9 mm. wide in *H. acutiloba*, averaging 5.95 mm.; 4.5-9 mm. wide in the intermediate types, averaging 6.65 mm. The averages of these measurements are summarized as follows:

	<i>H. americana</i>	<i>H. acutiloba</i>	<i>Intermediate</i>
Sepal length	11.6	11.75	12.05
Sepal width	6.5	6.75	7.15
Involucre length	12.3	11.4	11.4
Involucre width	7.25	5.95	6.65

Preliminary cytological studies conducted by Dr. O. J. Eigsti and Dr. Albert S. Rouffa revealed no conclusive differences between the two taxa.

STUDY OF HERBARIUM MATERIAL

In order to determine the relationship of North American *Hepatica* to other taxa of the genus, especially those involving the closely related *Hepatica nobilis*, specimens were studied by the senior author from the following herbaria: Chicago Natural History Museum, Gray Herbarium of Har-

vard University, Missouri Botanical Garden, and United States National Herbarium. To the curators of these institutions the senior author is deeply grateful for the privilege of studying this material. Criteria used for study involved length and pubescence of petioles, length and width of involucre and sepals, relative pubescence of leaf-blades and involucre, and shape and pubescence of achenes. Specimens of *Hepatica* from North America were compared with those from Europe and eastern Asia.

In Europe *Hepatica nobilis* consists of two main variations, (1) the more common type, with the lobes of the leaf-blades usually acute or short-pointed or acutish, and (2) a less frequent type, with the lobes of the leaf-blades usually rounded. The historical type is based upon the variation with acutish lobes and is the same as *Anemone Hepatica* L. var. *typica* (Beck) Gürke, *A. Hepatica* var. *acutiuscula* Pritzel, and *H. nobilis* var. *typica* Beck; the round-lobed variation is synonymous with *Anemone Hepatica* var. *rotundata* (Schur.) Gürke and *H. nobilis* var. *rotundata* (Schur.) Domin & Krajina. Since European authors are not in complete agreement as to whether such variations are forms or varieties of *Hepatica nobilis*, references to the European variations are indicated in the discussion below as round-lobed European *H. nobilis* and acute-lobed European *H. nobilis*.

Leaf-blade. Among the European collections of *H. nobilis* examined, about an equal number were either round-lobed or acute-lobed. Among the latter, a number of specimens are on the border line and have an appearance intermediate in aspect between *H. acutiloba* and *H. americana*. Among the round-lobed leaf-blades of the European *H. nobilis* are also a number of border line cases which exhibit a slight acuteness of the lobes. In some specimens, both types of leaf-lobes appeared on the same sheet (herb. *J. S. Mill*, May, 1839, Austria, in Gray Herbarium).

In general, the lobes of the leaf-blades of the American plants of *Hepatica* are sufficiently well-differentiated to enable one to distinguish two types (1) those with the lobes rounded at the summit and usually broader than long, the length of the leaf-blade being about two times the distance

from the base of the sinuses to the summit of the petiole, the usually accepted characteristics of *H. americana*, and (2) those with the lobes acute or acutish at the summit and usually longer than broad, the length of the leaf-blade being about three times the distance from the base of the sinuses to the summit of the petiole, the usually accepted characteristics of *H. acutiloba*. In various parts of the range where the two taxa meet, putative hybrids are encountered which cannot be placed in either *H. acutiloba* or *H. americana*. An example of this is represented by the collection of *Steyermark* 73114 from Reynolds County, Missouri (steep, north-facing wooded slopes along West Fork of Black River, T 32 N, R 2 W, sec. 1, southeast of West Fork P. O., 7½ mi. northeast of Bunker, April 26, 1952, in herb. Chi. Nat. Hist. Mus.). At this locality the uppermost acid chert slopes are occupied by *H. americana*, while the lower and middle limestone slopes are inhabited by *H. acutiloba*. Similar intermediate hybrid specimens were found in Carter County, Missouri, where both taxa are present, and in Lake County, northern Illinois, where the problem of intermediate plants presented itself to the authors at the outset of this study.

Forms of acute-lobed *H. nobilis* of Europe often resemble specimens of *H. acutiloba*, and, similarly, forms of round-lobed *H. nobilis* of Europe often markedly resemble plants of *H. americana*. It is, therefore, a matter of difficulty to distinguish some of the European forms of *H. nobilis* from one or the other of the two American taxa.

Petioles and scapes. Length of the petioles in *H. americana* varies from 4-15 cm. long in flowering specimens. In both the round-lobed and acute-lobed forms of *H. nobilis* of Europe, the petioles vary from 3-17 cm. long in flowering material. In *H. acutiloba* the petioles are slightly longer, varying from 6-20 cm. long.

The scapes of European *H. nobilis* in flowering specimens average somewhat longer than those of the American plants, equaling or surpassing the length of the petioles. The petioles and scapes of the European *H. nobilis* are usually less pubescent than those of the American plants, and especially of *H. americana*.

Sepal length. With respect to the length of the sepals, the

longest extremes were encountered in the European plants, the round-lobed form of European *H. nobilis* varying from 7-17 mm. long, averaging 10.17 mm., while the acute-lobed form of European *H. nobilis* varied from 7-18 mm. long, averaging 10.85 mm. In the American plants, the sepals of *H. americana* varied from 6-14 mm. long, averaging 10.1 mm., those of *H. acutiloba* varied from 6.5-15 mm. long, averaging 11.6 mm. It will be noted that the measurements of the sepals of dried specimens of the American taxa are shorter in their extremes of length when compared with those of living plants, the sepal length in living specimens of *H. americana* varying from only 9-13 mm. long and in living specimens of *H. acutiloba* from only 10-15 mm. long.

Sepal width. In the matter of sepal width, the measurements are as follows: in *H. americana* 3-7.5 mm. wide, with an average of 4.68 mm.; in *H. acutiloba* 3-7.5 mm. wide, with an average of 4.85 mm., being nearly the same in both taxa. On the other hand, the round-lobed form of European *H. nobilis* varied from 3-10.5 mm. wide, averaging 5.5 mm., while the acute-lobed form of European *H. nobilis* varied from 3.5-9 mm. wide, averaging 5.15 mm. Therefore, both forms of European *H. nobilis* have an average sepal width greater than either of the American taxa. Again, it is to be noted that the smallest measurements of living plants of *H. americana* and *H. acutiloba* were always greater than those of dried specimens of the same taxa, and the average width of both taxa was always greater than that of dried material.

Length of involucre: With regard to the length of the involucre, plants of American taxa have longer bracts of the involucre than those of both forms of European *H. nobilis*. In *H. americana* the bracts of the involucre varied from 6-16 mm. long, averaging 8.66 mm., while those of *H. acutiloba* varied from 8-18 mm. long, averaging 10.5 mm. In living plants of the American taxa, the average length of the bracts of the involucre was 12.3 mm. in *H. americana* and 11.4 mm. in *H. acutiloba*, the measurements for living specimens again being greater than those of dried specimens for the average length encountered. Among European specimens of *H. nobilis*, it was found that the bracts of the involucre were shorter than those of the American taxa, varying from 5-11

mm. long in the round-lobed form of European *H. nobilis* with an average of 7.58 mm., while the acute-lobed form of European *H. nobilis* ranged in measurements from 5-14 mm. long, with an average of 7.95 mm., the acute-lobed form having, therefore, a somewhat greater length than the round-lobed form.

Width of involucre. The width of the bracts of the involucre in both American taxa is greater on the average and in the extreme than that for both the round- and acute-lobed forms of European *H. nobilis*. In *H. americana* the width varies from 3-10 mm. wide in dried material, with an average width of 5.35 mm., and in *H. acutiloba* the width varies from 3-10 mm., with an average width of 5.05 mm. However, among the European *H. nobilis* the width of the round-lobed form ranges from only 3-6 mm. wide, averaging 4.25 mm., while the acute-lobed form ranges from 2.5-7.5 mm. wide, averaging 4.63 mm., therefore, being similar to the round-lobed form of *H. nobilis*. Both as to length and width of the bracts of the involucre, the American taxa of *Hepatica* exceed those of the European *H. nobilis* as regards not only average, but also the extremes in length and width.

The differences found between the American and the European taxa of *Hepatica* are tabulated in the following table:

	Involucre length	Involucre width	Sepal length	Sepal width
<i>H. americana</i> (dried)	6-16 8.66 (aver.)	3-10 5.35 (aver.)	6-14 10.1 (aver.)	3-7.5 4.68 (aver.)
<i>H. americana</i> (living)	9-17 12.3 (aver.)	7.5-9 7.25 (aver.)	9-13 11.6 (aver.)	5.5-8 6.5 (aver.)
<i>H. acutiloba</i> (dried)	8-18 10.5 (aver.)	3-10 5.05 (aver.)	6.5-15 11.6 (aver.)	3.5-7.5 4.85 (aver.)
<i>H. acutiloba</i> (living)	7-18 11.4 (aver.)	4-9 5.95 (aver.)	10-15 11.75 (aver.)	4-8 6.75 (aver.)
<i>H. nobilis</i> (round-lobed of Europe)	5-11 7.58 (aver.)	3-6 4.25 (aver.)	7-17 10.17 (aver.)	3-10.5 5.5 (aver.)
<i>H. nobilis</i> (acute-lobed of Europe)	5-14 7.95 (aver.)	2.5-7.5 4.63 (aver.)	7-18 10.85 (aver.)	3.5-9 5.15 (aver.)

Achenes. Fernald (Rhodora 19: 45. 1917) stated, "In *H. nobilis* of Europe the plump, conic-ovoid achene tapers to a short thick beak which is terminated by the sessile stigma.

In the American plant, on the other hand, the much more slender fusiform or lance-subulate achene is terminated by a very slender and definite, often curved, style." A study by the present author was made of those specimens of *Hepatica* in Europe and North America containing mature achenes in order to ascertain whether or not the differences mentioned by Fernald could be upheld. As relatively few achenes were available in the herbarium material examined, those of living plants were collected and studied.

Results of this study indicate that the American and European taxa cannot be distinguished by achenial differences as noted by Fernald. A specimen in the Gray Herbarium (mountainous woods near Innsbruck, Austria, May, 1839, herb. *J. Gay*) shows achenes with curved, slender styles. Another sheet in the Gray Herbarium (Alpes Mes Brianconnet, May 6, 1870, *M. Moggridge*) also shows a curved, slender style. The illustration of the achene and style in Hegi's *Illus. Flora von Mittel-Europa* (Band 3.3. *t.116, fig. 1b*) shows a type of slender style which can be matched in material from the United States. Some specimens from the United States may also exhibit ovoid achenes with relatively short styles in well-pressed and flattened specimens, and there appears to be no correlation between slender, lance-subulate achenes and slender, definite, often curved styles. The specimens cited above from the Gray Herbarium do not accord with Fernald's characterization of European material.

PRESENT INTERPRETATION

From a comparative study of *Hepatica* in Europe and North America, it is to be noted that much overlapping is encountered in measurements of involucre and sepals. Furthermore, there do not appear to be any achenial differences between the plants of Europe and North America. In general, it may be stated that the sepals of the American plants of *Hepatica* are narrower on the average than those of the European *H. nobilis*, that the involucre of the American plants are greater in both length and width on the average than in *H. nobilis*, that the petioles and scapes of the Euro-

pean plants are less pubescent than those of the American, and that the scapes of the European plants average somewhat longer than those of the American plants at anthesis.

The European *H. nobilis* exhibits similar variation with respect to differences in the apex of the leaf lobes as does the American material of the genus, perhaps less sharply so. The variation of the apex of leaf lobes in the American plants appears correlated also with similar variation in the apex of the bracts of the involucre. Aside from such differences, and in the corresponding leaf shape and proportion of leaf-lobing to the body of the leaf-blade, there is little else to use as distinguishing characters between the American taxa. Since the differences in relative length and width of involucre and sepals in *Hepatica* are measurable ones, it is believed that the American taxa can and should be kept distinct from the European, but as separate varieties, and not as separate species. It would seem more in keeping with a natural classification to treat the European and American taxa as conspecific under *H. nobilis*, the European plants being maintained as acute-lobed or round-lobed forms of *H. nobilis* var. *nobilis*, the American plants maintained as varieties of *H. nobilis*.

It is proposed, therefore, that the name of the European species, *Hepatica nobilis* Schreb., the oldest available valid specific epithet for the group under consideration, be used to include the later described American plants. As such, the American plants are here interpreted as American variations of a widely distributed species, *H. nobilis*. *Hepatica nobilis* var. *nobilis* becomes the name for the widely distributed European species, while *H. nobilis* var. *acuta* and *H. nobilis* var. *obtusa* become the names for the American plants formerly passing as *H. acutiloba* and *H. americana*.

Considered thus, *H. nobilis* with European and American varieties may be likened to similar cases of *Asplenium Ruta-muraria* L. var. *Ruta-muraria* and var. *cryptolepis* (Fern.) Wherry, *Polypodium vulgare* L. var. *vulgare* and var. *virginianum* (L.) Eaton, *Pteridium aquilinum* var. *aquilinum* and vars. *pubescens*, *latiusculum*, and *pseudocaudatum*, *Cypripedium Calceolus* L. var. *Calceolus* and var. *parviflorum*

(Salisb.) Fern. and var. *pubescens* (Willd.) Correll, *Linnaea borealis* L. var. *borealis* and var. *americana* (Forbes) Rehd.

The essential synonymy involved is as follows:

1a. **Hepatica nobilis** Schreb. var. **nobilis**, Spicil. Fl. Lips. 39. 1771 Based on *Anemone Hepatica* L. Sp. Pl. 538. 1753. *Hepatica triloba* Gilib. Fl. Lith. 2: 273. 1781; Chaix in Vill. Hist. Pl. Dauph. 1: 336 1786. *Anemone triloba* Stokes, Bot. Mag. Med. 3: 243. 1812. *Anemone Hepatica* var. *acutiuscula* Pritzel in *Linnaea* 15: 690. 1841. *Hepatica Hepatica* Karst. Fl. Deutschl. 559. 1883. *Hepatica triloba* var. *typica* Beck Fl. Nied.-Oesterr. 407. 1890. *Hepatica nobilis* var. *typica* Beck in Wiener Illustr. Gartenzeit. 21: 344. 1896. *Anemone Hepatica* subsp. I. *typica* var. α *typica* Ulbrich in Engl. Bot. Jahrb. 37: 270. 1906.

1b. **Hepatica nobilis** Schreb. var. **obtusa** (Pursh) Steyerm., comb. nov. Based on *Hepatica triloba* Gilib. α *obtusa* Pursh, Fl. Am. Sept. 2: 391. 1814. *Hepatica triloba* Gilib. var. *americana* DC. Syst. Nat. 1: 216. 1817. *Hepatica americana* (DC.) Ker in Edwards Bot. Reg. 5. t. 387. 1819. *Hepatica nobilis* f. *obtusa* (Pursh) Beck von Mannagetta, Wien. Illustr. Gartenzeit. 21: 349. 1896. *Hepatica nobilis* var. *obtusa* consists of the following five forms: **Hepatica nobilis** Schreb. var. **obtusa** (Pursh) Steyerm. f. **obtusa**. **Hepatica nobilis** Schreb. var. **obtusa** f. **candida** (Fern.) Steyerm., comb. nov. Based on *Hepatica americana* (DC.) Ker f. *candida* Fern. Rhodora 19: 46. 1917. **Hepatica nobilis** var. **obtusa** f. **purpurea** (Farw.) Steyerm., comb. nov. *Hepatica americana* f. *purpurea* Farw. Pap. Mich. Acad. 3: 97. 1924. Based on *Hepatica Hepatica* var. *purpurea* Farwell, Rep. Mich. Acad. 17: 169. 1916. **Hepatica nobilis** var. **obtusa** f. **rhodantha** (Fern.) Steyerm., comb. nov. Based on *Hepatica americana* f. *rhodantha* Fern. Rhodora 19: 46. 1917. **Hepatica nobilis** var. **obtusa** f. **Cahnae** (Farw.) Steyerm., comb. nov. Based on *Hepatica americana* f. *Cahnae* Farw. Pap. Mich. Acad. 3: 97. 1924.

1c. **Hepatica nobilis** var. β **acuta** (Pursh) Steyerm., comb. nov. Based on *Hepatica triloba* Gilib. β *acuta* Pursh, Fl. Am. Sept. 2: 391. 1814. *Hepatica acutiloba* DC. Prodr. 1: 22. 1824. *Hepatica triloba* var. *acutiloba* (DC.) Warne, in Am. Ent. & Bot. 2: 313. 1870. *Anemone acutiloba* (DC.) Laws. Rev. Canad. Ranunc. 30. 1870. *Hepatica acuta* (Pursh) Britton, Ann. N. Y. Acad. 6: 234. 1891. *Hepatica nobilis* f. *acutiloba* (DC.) Beck von Mannagetta, Wien. Illustr. Gartenzeit. 21: 349. 1896. *Hepatica nobilis* var. *acuta* consists of the following forms: **Hepatica nobilis** var. **acuta** (Pursh) Steyerm., f. **acuta**. **Hepatica nobilis** var. **acuta** f. **albiflora** (R. Hoffm.) Steyerm., comb. nov. Based on *Hepatica acutiloba* DC. f. *albiflora* R. Hoffm. Proc. Boston Soc. Nat. Hist. 36: 268. 1922. **Hepatica nobilis** var. **acuta** f. **rosea** (R. Hoffm.) Steyerm., comb. nov. Based on *Hepatica acutiloba* DC. f. *rosea* R. Hoffm. Proc. Boston Soc. Nat. Hist. 36: 268. 1922. **Hepatica nobilis** var. **acuta** f. **plena** (Fern.) Steyerm., comb. nov. Based on *Hepatica acutiloba* DC. f. *plena* Fern. Rhodora 49: 216. 1947.